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ABSORPTION OF THE HYDRANTH IN HYDROID POLYPS.

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In 1900 there appeared a paper[1] by Professor Loeb on the "Transformation and Regeneration of Organs," the first part of which contained a discussion of the process of absorption in campanularia hydroids. His results were obtained from a study of the effects produced on the polyps by placing them in shallow dishes of sea water, so that they were in contact with the glass; under these conditions he found that they were gradually transformed and at length absorbed completely into the stem. To summarize briefly Loeb's account of this process, he states that there is noticeable first a contraction of the animal into the cup, followed by the fusion of the tentacles and later by the withdrawal of the whole polyp — now a shapeless mass of protoplasm — into the stem. This complete transformation he ascribes to contact, since it "is certain that contact with sea-water favors the formation of polyps with their more solid elements, while the contact with solid bodies favors the formation of the more fluid material of the stem or stolon." It seemed probable that a histological examination of these changes, in which the hydroid is represented as transforming and *creeping back into the stem*, might prove of interest, since they involved a complete transformation of well-differentiated structures. Therefore, at Professor Morgan's suggestion, I worked on this subject at Woods Holl during the summer of 1902. I was able to obtain a table first through the kindness of the director, and later was appointed to the Bryn Mawr table.

On examining the literature it will be found that there are frequent references to the absorption or disappearance of polyps. Loeb finds for *Margelis* and *Antennularia* that the polyps

[1] *The American Journal of Physiology*, IV., 1900.

"disappear" when their condition of growth is disturbed — *i. e.*, the former being brought into contact with a solid, the latter being suspended horizontally so that its relation to gravity is changed. *Eudendrium*, according to some workers, sheds its hydranths when brought into the laboratory, but I have also often found absorption occurring under the same conditions, and *Eudendrium tenue*, a smaller and more delicate form than *Eudendrium racemosum*, responds in this way even more constantly. *Pennaria*[1] has recently been examined by Cerfontaine who finds that the day after the hydroids have been collected "ca matérialse trourait dans un mauvais état, les polypes qui persistaient étaient morts, les parties mollas s'étaient retireés dans la perisarque et les extremitées du cœnosarque réduit s'étaient cicatricées. Si l'ou conserve les branches, en maintenant une circulation d'eau de mer, ou les voit souvent reprendre de la vigueur. . . . Ou peut de cette façon déterminer expérimentalement une repetition de la regeneration spontanée. A la suite des troubles brusques produits dans les conditions d'être de ces organismes, par la récolte, le transport, le changement d'eau, le changement de température, de lumière, etc., ou determine rapidement la destruction des polypes ; mais bientôt, il semple se produire une acclimation rapide, et aussitôt une nouvelle régénération commence." *Tubularia* never absorbs its polyps but sheds them soon after being collected, and after a day or so if undisturbed, new polyps grow out from the old stalk, a new growth of stalk also taking place behind the head.

It seemed possible that the absorption of the heads of *Campanularia* might be analogous to that in these other forms, in which case it should occur even when not in contact with solids. To test this, I left the hydroids still growing on bits of wood, and placed them in the dishes, so that they were completely surrounded by water. Nevertheless the polyps began to absorb and by the end of twelve hours had almost entirely disappeared, while a few new ones were beginning to form from the old stalks. I also noticed on examining dishes of unused hydroids that had been standing over night, a large percentage of absorbing polyps.

[1] "Recherches expérimentale sur la Régénération et l'Hétéromorphose chez astroides calycularis et Pennaria Carolinii," *Archives de Biologie*, XIX., 1902.

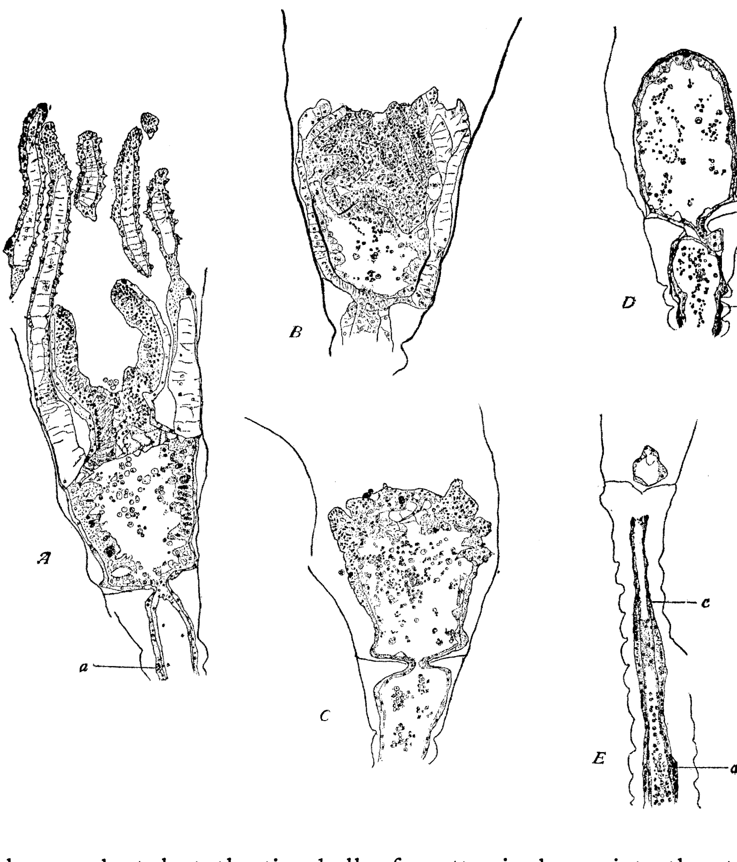
These results show that contact cannot in any case be considered the only factor to which the absorption of campanularian polyps is due, and that the process closely resembles that in other polyps in which under similar conditions we find either absorption or direct shedding of the hydranths with subsequent regeneration.

The material for study was obtained fresh each day, so that the animals should be in thoroughly good condition. Pieces of *Campanularia* were then cut and laid in watch crystals in contact with the glass in the way described by Loeb. The stages in the absorption of *Eudendrium* and *Pennaria*, which I used for comparison, being more difficult to obtain, were taken whether in contact or not, according to where they presented themselves. All the material was killed in cold corrosive acetic, and stained with Delafield's hæmatoxylin and congo red.

Within a few minutes after the removal of a piece or stalk, the cut end closes over, and the digestive current begins to flow slowly from one end of the hydroid to the other. It passes forward, and then is driven backward mainly by the contraction of the circular muscles of the polyps in the region just below the tentacles, but not involving a contraction of the whole animal; a slight pause occurs between each change in direction. The irregularity in the contraction of the polyps sometimes complicates the course of the current. At first the polyps remain expanded, and the only change noticeable is in the digestive fluid which becomes more and more laden with spherical granules of all sizes. The current is sometimes driven with such force that the contents break their way through a newly formed stolon or through the mouth of the polyp. The animal has up to this time been fully expanded except for the rhythmic contractions which decrease only the diameter of the body, but now it gradually contracts into its cup, and the body becomes shorter and broader, the latter change being largely due to the thickening of the ectoderm as can be seen even in the living animals. The tentacles undergo excessive contraction, becoming a crown of mere stubs, and then disappear altogether; their cells passing into the cavity of the polyp. At the same time, the hypostome absorbs.

These changes take some time and normally occupy at least

two thirds of the time required for the complete disappearance of the polyp; sometimes the digestive current may, at this stage, distend the degenerating polyps and delay absorption for several hours. The usual time required is from six to twelve hours, but under the same conditions it may last from one to two days. The size of the structure left in the cup becomes slowly less and



less, and at last the tiny ball of matter is drawn into the stem. I examined the living material carefully for signs of the breaking of the protoplasmic threads that stretch from the cœnosarc to the perisarc just below the cup, but I was unable in most cases to find any trace of it, until the last stage. At that time the strands break and the cœnosarc is drawn out in a fine thread. The protoplasm has been under a strain for the greater part of

the time, due to the growth of the stolon, but the protoplasm of the polyp cannot apparently be *drawn* through into the stem until it has reached a certain stage in its absorption.

The finer structure of normal *Campanularia* is as follows: The ectoderm cells which are flat on the body become cubical on the hypostome; there are no nettle cells except an occasional wandering one, until we come to the upper half of the tentacles. Below the cup lie masses of nettle-forming cells, somewhat irregular in their position, but never found in an quantity anterior to the first annulation. The endoderm is well differentiated on the hypostome into deeply-staining goblet cells and long spindle-shaped cells; in the walls of the body cavity there are large, clear endoderm cells and smaller granular gland cells. The tentacles contain a single row of endoderm cells. These are separated from those of the body cavity by a lamella at the base of the tentacle. Signs of change first arise in the endoderm of the body and the digestive current becomes filled with degenerating endoderm and gland cells, pinched-off portions of cytoplasm and loose nuclei. This process continues for some time without the appearance of any other change, except that as the endoderm becomes less, the lamella slowly contracts, becoming correspondingly thicker, and the ectoderm, having less surface to cover, changes from a thin layer to a much thicker one. The tentacles have also contracted to an abnormal extent, and at last by the breaking of the lamella across their base the endoderm cells round up and pass out into the body cavity. At this stage the tentacles are crowded together, and, the ectoderm being thrown into folds by the excessive contraction, frequently give, in surface view, the effect of being fused, as stated by Loeb. But by careful study the independence of the tentacles can be traced in spite of the closeness with which they are pressed together.

Soon after the endoderm has begun to pass out from the tentacles the lamella breaks near the tip and masses of nettle and ectoderm cells are poured into the cavity. The hypostome also degenerates, the ectoderm cells passing out rapidly into the digestive current and the lamella contracting after them. Soon the lamella of the hypostome breaks and disappears and the mass of ectoderm is also turned in. The polyp is now simply a shell of

ectoderm and endoderm which are separated by the elastic lamella, which usually meets more or less completely at the oral end after the material of the tentacles and hypostome has been absorbed. At this time the lamella breaks in places and more cells from the ectoderm pass through. There is also a small amount of degeneration on the outside, and by these means the amount of ectoderm rapidly diminishes. Gradually the structure becomes smaller and smaller and finally the last fragment is drawn out of the cup. If there are many cells loose in the body cavity of the polyp at this time, they frequently break through the thin wall and pass out into the water.

The best guide by which to determine the amount of protoplasm drawn into the stem, was found to be the masses of nettle-forming cells before alluded to. The cells really drawn represent a very small fraction of the original number. The greater majority have been thrown into the digestive current, from which many are absorbed by the endoderm cells throughout the entire colony.

To compare the process in *Campanularia* with that in other hydroids, I examined both *Eudendrium* and *Pennaria* in which "absorption" also occurs and found the process again one of degeneration. From the time when the first degenerating masses are seen in the digestive current to the final drawing through of the small degenerated mass, the method is almost identical with that in *Campanularia*.

Recently there has appeared a paper by Gast and Godlewski, Jr., on the degeneration of the polyps of *Pennaria*[1] who have obtained results similar to my own.[2] It is interesting to note that their material was taken from polyps which had regenerated their heads in the laboratory, and then after two or three days had begun to absorb again — a different condition from that under which mine were obtained, yet the process is the same. Since these investigators have fully covered the ground for *Pennaria*[3] I shall not describe the changes in that form and indeed merely speak of two or three points in the degeneration of *Eudendrium*

[1] "Ueber den Regulationsersheinungen bei Pennaria carolinii," *Archiv für Entwickelungsmechanick der Organismus*, XVI., 1903.

[2] See preliminary note, BIOL. BULL., IV., 2, 1903.

[3] Probably another species.

that differ from that in *Campanularia*. The degeneration of the endoderm is much more rapid, the cells breaking down more completely and filling the digestive cavity with fine protoplasmic granules. Since there is no lamella across the bases of the tentacles, the endoderm can also pass out from them more readily. The loss of ectoderm is here also accomplished by the passing in of cells through breaks in the lamella, the edges of which are apt to draw together again. The complete disappearance of the lamella does not occur until a very late stage. At the end the whole of the remaining structure is not always drawn through into the stalk, but an ill-defined mass of protoplasm is often left at the end.

The constant position of the ectodermal gland cells near the beginning of the stalk throughout the degenerative changes show that there is no drawing of cells into the stem until the final stages.

The histological evidence thus supports my observations on the living animals, that in *Campanularia* we have to do with no transformation of the protoplasm due to contact, but with a degeneration of the polyp. Similar changes take place in other hydroids, and occur apparently when they are subjected to abnormal or harmful conditions.

I wish to express my thanks to Professor Morgan for his suggestions and kind supervision of my work.